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Peltaspermalean seed ferns with preserved cuticle from the Upper Triassic Karamay Formation in the Junggar Basin, northwestern China

Xuezhi He[1, 3], Tianming Shi[5], Mingli Wan[3], Shijun Wang[2], Jason Hilton[4], Peng Tang[3], Jun Wang[3, 6]*

[1]*Anhui Geological Museum, Hefei 230031, PR China.*

[2]*State Key Laboratory of Systematic and Evolutionary Botany (LSB), Institute of Botany, Chinese Academy of Sciences, Beijing 100093, PR China*.

[3]*State Key Laboratory of Palaeobiology and Stratigraphy (LPS) and Department of Palaeobotany and Palynology, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, PR China*.

[4]*School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK.*

[5]*Research Institute of Experiment and Detection, Xinjiang Oilfield Company, PetroChina, Karamay 834000, P.R. China.*

[6]*University of Chinese Academy of Sciences, Beijing 100049, PR China*

*Corresponding author

Highlights:

1) New species of *Scytophyllum* described from the Upper Triassic of the Junggar Basin.

2) The species is distinguished by interfascicular veins.

3) Thick cuticles with sunken stomata and abundant papillae indicate water stress.

4) Leaves have a stomatal index of 3.27–5.25 and stomatal density of 15–30.

5) Comprehensive comparison undertaken between all species of *Scytophyllum.*

Abstract

Foliage of a new peltaspermalean seed fern is described on the basis of a large collection of well-preserved plant adpressions with cuticle from the Upper Triassic Karamay Formation in Xinjiang Province, NW China. Pinnae are lanceolate with undulate-dentate margins and with fascicular lateral veins in lobes. Tertiary veins are simple as are interfascicular veins that occur between fascicular lateral veins. Cuticles are thick, amphistomatic, with abaxial and adaxial cuticles being similar to each other and having clear costal and intercostal areas. Stomata are sunken and randomly distributed on both the abaxial and the adaxial cuticle. The stomatal complex is monocyclic and comprises 4–7 subsidiary cells. Papillae are present on ordinary cells and on subsidiary cells surround the stomatal aperture. The adaxial leaf surface has a stomatal index of 3.27 and an average stomatal density of 15 per mm^2, whereas the abaxial surface has a stomatal index of 5.25 and an average stomatal density of 30 per mm^2. This is the first report of the cuticular structure of *Scytophyllum* from the Junggar Basin, which now enables detailed comparison with other species of the genus from Eurasia. Analysis of the sedimentary succession containing *Scytophyllum* suggests a humid or seasonally dry environment, but the thick cuticles with sunken stomata and abundant papillae indicate that the plant was adapted to living in water-stressed conditions.

Key words: *Scytophyllum*, *Aipteris*, pteridosperm, epidermis, Xinjiang

1. Introduction

The Junggar Basin is one of three large sedimentary basins in Northwest China's Xinjiang Uygur Autonomous Region (Fig. 1) and is of considerable economic importance due to its vast oil, natural-gas, and coal resources (Tang et al., 1997). Research on Mesozoic plant fossils from the basin began in the early 20th Century with Seward (1911) documenting an assemblage based on specimens previously collected by Obrutschew in 1905–1906. Since that time plant fossils within the basin have been extensively studied in the course of regional geological surveys and resource exploration, primarily to facilitate biostratigraphic correlation (e.g., Sze, 1953, 1956a,b; Yang et al., 1986; Sun et al., 2010). Within the basin, Permian-Triassic plants are comparatively well-known and floral assemblages are now well established (Table 1; Yang et al., 1986). Whereas isolated examples of *Pecopteris* sp. occur in the Jiucaiyuan Formation (Yang et al., 1986), the stratigraphically lowest floral assemblage including multiple species is the Anisian to Carnian *Danaeopsis-Bernoullia* assemblage (Table 1) mainly occurs in the Karamay Formation in the Dalongkou section at Jimsar (Yang et al., 1986). The overlying Upper Triassic floras from the Junggar Basin consist of two floristic assemblages (Table 1), namely the *Danaeopsis-Nanzhangophyllum* assemblage from the Huangshanjie Formation dated to the Carnian-Norian stages of the Triassic, and the *Glossophyllum-Cycadocarpidium* assemblages from the Haojiagou Formation dated to the Norian-Rhaetian stages of the Triassic (Sun et al., 2010).

The genus *Scytophyllum* Bornemann, the index plant of the *Scytophyllum* Flora is

widely distributed in Russia and Europe during the Triassic (Dobruskina, 1994). Its leaves commonly occur association with peltaspermalean reproductive organs (Dobruskina, 1969; Kustatscher et al., 2007), and similarities of cuticle structure in *Scytophyllum* and the peltasperm *Lepidopteris*, including the type of stomatal apparatus and number of the subsidiary cells indicate that *Scytophyllum* was most likely a peltaspermalean pteridosperm (e.g., Bateman and Hilton, 2009). *Scytophyllum* was recognized for the first time within the Junggar Basin by Shi et al (2014) who documented *Scytophyllum* sp. from the Karamay Formation at the Dalongkou section (Fig. 1b). Unfortunately, the specimens documented by Shi et al. (2014) were imperfectly preserved and showed neither venation nor cuticular details, so that their identification to species level was not possible.

During fieldwork in 2013 we collected specimens of *Scytophyllum* with preserved cuticle from the Karamay Formation to the north of Karamay City (Fig. 1). In the present paper we describe these specimens as a new species and provide detailed comparisons to other species of the genus. *Scytophyllum karamayense* sp. nov. adds additional information about the floristic assemblage from the Karamay Formation and its floristic relevance to Triassic floras worldwide. Evaluation of sedimentary facies and cuticle analysis enabled us to infer the palaeoecology of *Scytophyllum* from the Junggar Basin.

2. Geological Setting

The Junggar Basin (Fig. 1a) is located on the Junggar Plate, which was a part of

the eastward extension of the Kazakhstan Plate that separated from the Siberian Plate during the early Paleozoic (Zhou et al., 1995).

[Approximate position of Figure 1 and Table 1]

In the Junggar Basin, Mesozoic non-marine deposits are extensive and well exposed, containing abundant floral and faunal remains (Sze, 1956a, b; Deng et al., 2000; Sun et al., 2001, 2010). Palaeophytogeographically, the Upper Triassic Junggar flora has previously been considered part of the "Northern China Flora" containing the *Danaeopsis-Bernoullia* assemblage (Dobruskina, 1994; Sun et al., 1995, 2001, 2010). The Karamay flora of the Northwestern Junggar Basin includes *Danaeopsis fecunda*, *Neocalamites carrerei*, *N. annularioides*, *N. carcinoides*, *Bernoullia zeilleri*, *Taenioclaopsis* cf. *rhizomoides*, *Thinnfeldia nordenskjoeldii*, and *Cladophlebis shensiensis* (Luo et al., 2015). The presence of *Danaeopsis fecunda* and *Bernoullia zeilleri*, which are the typical elements of Late Triassic Yanchang flora and the *Danaeopsis-Bernoullia* assemblage, indicates that the Karamay flora is part of the "Northern China Flora" (Luo et al., 2015).

Specimens of *Scytophyllum* documented here were collected from the lower part of the Karamay Formation in the Shendigou section (N 45°43.637′ E 84°59.540′) (Fig. 1b, c, d). In this section the Late Triassic Karamay Formation unconformably overlies Carboniferous metamorphic rocks (Table 1; Luo et al., 2015), whereas elsewhere in the basin the Early Triassic Shaofanggou and Jiucaiyuan formations occur intercalated

between the Carboniferous basement and the Karamay Formation (Table 1; BGMRX, 1993; Tang et al., 2015).

The sedimentary succession in the Karamay Formation at the Shendigou section comprises, from the bottom to the top, sandy conglomerate containing fossil plants, muddy conglomerate, fine sandstone, siltstone and claystone (Fig. 1 e). Several red-beds are intercalated in the succession (Fig. 1 e, f). The sediments overall represent a fining upwards succession, marking decrease in depositional energy. Sedimentary and lithological analyses indicate that the plant remains are preserved in an alluvial fan facies, with the entire succession beginning with an alluvial fan system developing facies into fluvial and then lacustrine facies (Fig. 1e; BGMRX, 1993; Tang et al., 2015). The plant remains co-occurring with *Scytophyllum* include *Neocalamites* cf. *hoerensis* Halle, *Todites goeppertianus* Krasser, *Cladophlebis kaoiana* Sze, *Pterophyllum nathorstii* Schenk, *Baiera* sp., *Glossophyllum* sp. and *Taeniopteris richthofenii* Sze. Although *Danaeopsis* and *Bernoullia* are absent in the current assemblage, the flora from the Karamay Formation at the Shendigou section is otherwise similar to the Yanchang Flora, and belongs to the Upper Triassic *Danaeopsis-Bernoullia* Floral Assemblage (Luo et al., 2015).

3. Materials and methods

The specimens are preserved as impressions and compressions with well-preserved cuticle, but are very fragmentary, most remains representing isolated single pinnae. Only a few specimens preserve penultimate pinnae. As large cuticles

provide more epidermal anatomical information (Kerp, 1990), entire pinnae were prepared for cuticular analysis. From the Shendigou section cuticles readily detaches from the rock matrix when the slabs dry out, but in some instances dissecting needles were applied to isolate cuticles from the matrix.

Isolated cuticles were macerated using 20% hydrochloric acid for 24 hours and then in 30% hydrofluoric acid for 24 hours to dissolve adhering rock fragments. The cuticles were then neutralized and cleaned by immersion in gently running water, and finally treated with Schulze's reagent (HNO_3 with a concentration of 68% and $KClO_3$) for 45 to 50 seconds before neutralizing by washing in distilled water.

For study by light-microscopy, individual cuticles were mounted in glycerine jelly on glass slides, and sealed with nail polish under a coverslip (modified after Kerp, 1990; Kerp and Krings, 1999). For study by scanning electron microscopy (SEM), the cuticles were dehydrated in alcohol (in a successive series from 50%, 75% and 99.9%), and then mounted on SEM stubs using double-sided adhesive tape. Unfortunately, the adaxial and abaxial cuticle of the apex of one pinna became detached during preparation for which the pieces were subsequently prepared separately.

[Approximate position of Figure 2]

Macrophotography was undertaken using a Nikon D800 digital camera with a 60 mm macro lens. Large cuticle preparations were photographed in an artificial light

system to show the veins (Figure 2; the technique is modified after Rowe, 1999 and Kerp and Bomfleur, 2011). The slide is fixed vertically and a light beam of a directional lamp directed obliquely through the slide in order to highlight the veins (Figure 2). Microphotographs were made using a Leica DM5000 compound microscope with transmitted light and a Leica DC 500 digital microscope camera system. SEM analysis was undertaken using a Hitachi S4800 SEM. For illustrating the gross morphology of the cuticle, photos of the top and basal part of cuticles were stitched together using Photoshop version CS 5.

Terminology for describing cuticular structures follows Dilcher (1974) and Kerp (1990). Following Mamay et al. (2009), the term "interfascicular vein" is applied for describing the tertiary veins directly arising from the midrib between adjacent fascicle.

4. Results

4.1. Systematic palaeobotany

Gymnospermae

Family Peltaspermaceae Pilger et Melchior, *in* Melchior and Werdermann 1954

Genus *Scytophyllum* Bornemann, 1856

Species *Scytophyllum karamayense* sp. nov.

Holotype: PB 21736.

Repository: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Type locality: Shendigou section, Karamay City, Xinjiang (N 45°43.637′ E 84°59.540′).

Stratigraphic position: Karamay Formation.

Age: Late Triassic (Carnian-Rhaetian).

Etymology: The specific epithet refers to Karamay City where the type material was collected.

Diagnosis: Frond at least once pinnate, coriaceous. Pinnae lanceolate, with acute apex and with undulate to dentate margin. Pinna midrib straight, thick; lateral veins forming pinnate fascicles in pinna lobes; simple interfascicular vein between lobes. Secondary and tertiary veins weak. Pinnae amphistomatic, costal and intercostal areas distinct, with elongate and longitudinally aligned cells in costal areas and with smaller and more isodiametric cells in intercostal areas. A abaxial cuticle with higher stomatal density and stomatal index. Stomatal apparatus small, round or pentagonal. Papillae raised direct, surrounding the stomatal aperture.

4.2. Description

4.2.1. Gross morphology

Only incomplete fronds have been encountered, the largest of which is a 65 mm wide, 30 mm long specimen with a 2.5 mm thick rachis that bears two pairs of opposite pinnae (Plate I, 1, 2). The pinnae are incomplete with only the basal regions preserved, and are characterized by a coriaceous lamina. The upper two pinnae demonstrate that the midrib is slightly decurrent. The catadromous base of the upper

right pinna and the anadromous base of the lower left pinna are constricted. The lower left pinna (Plate I, 1) is the most complete example recorded. It is approximately 30 mm long and 10 mm wide and has a preserved dentate margin. The venation is indistinct on the macrofossil prior to cuticle preparation (Plate I, 1, 2).

[Approximate position of Plate I]

The midrib on the adaxial cuticle is straight and approximately 1.5 mm wide. The secondary and tertiary veins are weak and form a bipinnate pattern (Plate I, 3, 4). Secondary veins are pinnate on the midrib, while tertiary veins are pinnate on secondary veins. Three to five pairs of tertiary veins attach to the secondary vein at an acute angle forming a fascicle. Each fascicular vein bundle corresponds to a tooth on the margin (Plate I, 3, 4). Interfascicular veins are inserted between the fascicular veins and corresponds to the sinus between adjacent teeth (Plate I, 3, 4, arrow). The position of the interfascicular vein is weakly marked on cuticular preparations and is difficult to distinguish from the surrounding cells. The adaxial cuticle is conspicuously thickened along the pinna margin. (Plate I, 5).

[Approximate position of Plate II]

The fascicular vein complexes and the interfascicular veins are distinct on the cuticle (Plate II). The midrib is straight and covered by small, isodiametric cells (Plate

II, arrow P). Secondary veins are much weaker than the midrib, arising from the midrib at angles of approximately 45° (arrow S in Plate II). Tertiary veins are produced at angles of approximately 30° and are thin, short and do not bifurcate (arrow T in Plate II). Interfascicular vein impressions of the cuticles are conspicuous and the cells covering the interfascicular veins have different shapes and arrangement from those of the costal and intercostal areas (black arrow in Plate II): cells on the interfascicular veins are small, pentagonal-polygonal, and well cutinized; near the margin, cells on the interfascicular veins become even smaller and more elongate–pentagonal.

4.2.2. Adaxial and abaxial cuticle (Plate III - IV)

Adaxial cuticle (Plate III)

In the costal area cells are generally about 90 x 30 μm, with longitudinal axes regularly arranged in lines parallel to the vein course (Plate III, 1). The costal area is 5 to 16 cells wide (arrows in Plate III, 1, 2). In the intercostal area, cell shape and size varies from isodiametric to elongate polygonal and from 30 x 30 – 60 x 90 μm (Plate III, 1). Cell long axes in intercostal areas are parallel to the costal area. In larger intercostal areas (Plate III, 2), the cell arrangement becomes increasingly random towards the center of the intercostal area. The long axes of the cells in the center of intercostal area are orientated vertically to adjacent vein courses (Plate III, 2). Cells near the midrib are small, square to elongate-rectangular, and approximately 30 x 30 – 30 x 50 μm (Plate III, 3 arrow), with cell size gradually increasing away from the

midrib. Cells on the midrib are elongate polygonal and in some cases isodiametric, with sizes varying from 30 x 30 – 30 x 70 μm (right part of Plate III, 3).

Near the pinna margin, cells in the zone between adjacent vein bundles are arranged in an arc (Plate III, 4, white arrow). In the costal area (Plate III, 4 black arrows) cell orientation anastomoses at the interfascicular vein (arrows in Plate III, 4).

Stomata are randomly distributed in both costal and intercostal areas and have a denser spacing in the intercostal area and on the midrib (Plate III, 1–4). Stomata are sunken and the guard cells are not visible (Plate III, 5–6). The stomatal apparatus are small, isodiametric, rounded or pentagonal, and composed of 4–6 (normally 5) subsidiary cells (Plate III, 5-6). Even adjacent stomata do not share any subsidiary cells (arrows in Plate III, 5). Subsidiary cells are trapezoidal, with proximal and radial walls strongly cutinized (Plate III, 5-6). Most ordinary epidermal cells bear a single papilla that is usually solid (Plate III, 5), rarely hollow (Plate III, 6). Papillae on subsidiary cells are raised and directly surround the stomatal aperture (Plate III, 5–6). The anticlinal walls are straight and sometimes irregular thickenings form a hair-like pattern (Plate III, 5, arrow). The stomatal index of the adaxial cuticle is 3.27, and the average stomatal density is 15 per mm^2.

[Approximate location of Plate III]

Abaxial cuticle (Plate IV)

The abaxial cuticle is thinner than the adaxial cuticle, and the costal and intercostal areas are less clearly differentiated. Cells in the costal area are isodiametric to

elongate-polygonal; and are smaller but otherwise similar to those on the adaxial cuticle (Plate IV, 1). The size of the cells is about 30 x 70 μm, with cell long axes in the costal area arranged in lines parallel to the vein course (arrows in Plate IV, 1) whereas they become smaller and more isodiametric forming acute angles with the costal area in the intercostal area (Plate IV, 1, 2). Near the midrib, cells in the costal area are small, isodiametric polygonal or slightly elongate, varying from approximately 30 x 30 – 50 x 50 μm (arrow in Plate IV, 2). On the midrib, most of the cells are isodiametric polygonal or rectangular (right part of Plate IV, 3). Near the pinnule margin, cells are small and slightly elongate, with long axes orientated parallel to the margin and in the same orientation as those on the adaxial cuticle (Plate IV, 4). Stomata are randomly distributed in the costal and intercostal areas, whereas they are more common in the intercostal area (Plate IV, 1–4). Stomata are, like those in the adaxial cuticle, are pentagonal, sometimes round, and measure approximately 50 μm in diameter (Plate IV, 5–6). Anticlinal walls are straight and may in some cases bear irregular thickenings (Plate IV, 5–6). Papillae on ordinary epidermal cells are usually solid (Plate IV, 1–4), whereas those on subsidiary cells are usually hollow papillae and raised prominently to surrounding the stomatal apertures (Plate IV, 5–6). The stomatal index of the abaxial cuticle significantly higher (5.25) compared to the adaxial cuticle, and the average stomatal density is about 30 per mm^2.

[Approximate location of Plate IV]

4.2.3 SEM observations (Plate V)

Exterior cuticle surface

Papillae are indistinct on the ordinary cells surrounding the stomatal complex (Plate V, 1), although periclinal walls of cells surrounding stomata may be diffusely thickened. The stomatal aperture is surrounded and at least partially covered by a star-shaped cluster of 4–5 papillae (Plate V, 1 arrow, 2). The stomatal aperture can be observed among the papillae (Plate V, 2).

Interior cuticle surface

Guard cells, which are not readily observed under transmitted light microscopy, are distinct on the interior of the cuticle under the SEM. They are very small, kidney-shaped, approximately 6 x 17 μm in dimension, and are surrounded by six trapezoidal subsidiary cells. The radial and tangential walls of the subsidiary cells are thick and strongly cutinized (Plate V, 3). Anticlinal walls seem slightly sinuous under transmitted light (Plate III, 5; Plate IV, 5–6), but appear generally straight and irregularly thickened using SEM (Plate V, 3–6). Holes on the interior cuticle surface of periclinal walls of the subsidiary cells indicate hollow papillae (Plate V, 3) as shown in Plate III, 6. Such holes are rare on the periclinal walls of the ordinary cells, indicating the hollow papillae seldom occur on ordinary cells (Plate IV, 4).

[Approximate location of Plate V]

4. Discussion

4.1. Comparison

The present material can be assigned to the peltasperm foliage genus *Scytophyllum* Bornemann based on the bipinnatifid architecture, coriaceous lamina, characteristic venation with fascicular vein bundles and simple interfascicular veins, and cuticular features with stomatal complexes surrounded by papillate subsidiary cells (Bornemann, 1856; Linnell, 1933; Dobruskina, 1969). To some degree, it is also similar to other foliage genera common in the Permian and Triassic, i.e., *Fascipteris* Gu et Zhi, *Comia* Zalessky, *Auritifolia* Chaney et al., *Lepidopteris* Schimper emend. Townrow, *Dejerseya* Herbst emend. Bomfleur, *Pachypteris* Brongniart, *Aipteris* Zalessky and *Aipteridium* Li et Yao.

Fascipteris and *Validopteris* form vein bundles that are very similar to those of *Scytophyllum* (Dobruskina, 1969), however, both have much more delicate leaf and cuticle substance, and bear prominent lateral veins.

Comia and *Auritifolia* are Permian peltaspermalean seed plant, lateral veins of which form fascicular and interfascicular veins that are very similar to those of *Scytophyllum*. The different is the lateral veins of *Comia* are much denser and terminate at the pinna margin, but those of *Scytophyllum* are not (Mamay et al., 2009). *Auritifolia* differs in having coarse venation, most tertiary veins of which may anastomose (Chaney et al., 2009).

Foliage of the Mesozoic peltaspermalean pteridosperm *Lepidopteris* has similar leaf and cuticular structure to the species described here (Dobruskina, 1969;

Kustatscher et al., 2011). However, *Lepidopteris* differs in having a lumpy rachis bearing characteristic blister-like swellings, and in having intercalary pinnules that are absent in species of *Scytophyllum* (Dobruskina, 1969).

Dejerseya is a Gondwanan Triassic peltasperm with pinnatified and partly pinnate lamina that generally resembles those of *Scytophyllum* (Bomfleur et al., 2011). Although *Dejerseya* and *Scytophyllum* share similar venation patterns and cuticular features, *Scytophyllum* is distinguished by its gross morphology in which its foliage has a characteristic venation pattern in which the secondary and tertiary veins do not reach the leaf margin but end blindly within the lamina (Dobruskina, 1969, 1975; Morel et al., 2010; Bomfleur et al., 2011). However, in the current specimens, cuticular analysis shows that in the costal areas secondary and tertiary veins sometimes reach the margin of the pinna. Except for the pinna margin, vein patterns and cuticular features of *Dejerseya* and *Scytophyllum* are otherwise distinct based on the leaf framework and ultimate pinna shape. The *Dejerseya* frond is pinnatifid to partly pinnate, whereas *Scytophyllum* frond is at least bipinnate. The widest part of the *Dejerseya* ultimate pinna is in the middle, whereas the widest part of the *Scytophyllum* ultimate pinna is generally occurring towards the base.

[Approximate location of figure 3]

In *Scytophyllum* and *Pachypteris* venation consists of a prominent vein that produces inconspicuous laterals (Taylor et al., 2009); *Pachypteris*, however, can be

distinguished by a thick or abaxially folded lamina and by essentially dichotomizing (instead of pinnately branched) vein bundles.

Aipteris was established for gigantopterid plants from the Cisuralian (early Permian) of the southern Urals (Zalessky, 1939). However, the type species *Aipteris speciose* was poorly defined and the holotype specimen was lost. Subsequently described species assigned to *Aipteris* are from the Triassic (Brick, 1952; Neuburg, 1959; Sixtel, 1961, 1963). Dobruskina (1969, 1975, 1982) considered the genus *Aipteris* invalid, and transferred the then-known species of *Aipteris* into either *Scytophyllum* or *Vittaephyllum* Dobruskina, 1975. Following Dobruskina (1969, 1975, 1982), we conclude that the Chinese species *Aipteris obovata* Huang et Zhou, *A. shensiensis* Huang et Zhou and *A. wuziwanensis* Huang et Zhou from the Triassic of Shaanxi Province in China (Huang and Zhou, 1980), of which the pinna midrib is not bifurcate as in *Vittaephyllum*, should be transferred to the genus *Scytophyllum*.

Li and Yao (1983) in their review of gigantopterid plants found that the winged rachis of *Aipteris pinnata* was very different from those of *Aipteris speciosa* leading them to create the genus *Aipteridium* with the type species *Aipteridium pinnatum*. *Aipteridium* leaves have almost the same vein pattern as *Scytophyllum*, but with different reproductive organs; the seeds of *Aipteridium* are born on both sides of the midrib (Yao and Wang, 1991).

Species of *Scytophyllum* have previously been attributed to foliage of the Mesozoic peltaspermalean pteridosperms (Dobruskina, 1969; Kustatscher et al., 2011). *Scytophyllum* is widely distributed in Upper Triassic strata of Eurasia, where it is

considered as an index fossil for the *Scytophyllum* flora (Dobruskina, 1994; Kiritchkova and Esenina, 2014).

[Approximate location of table 2 and 3]

To date, 27 species of *Scytophyllum* have been documented from Asia, Europe, southern Africa and South America (Tables 2 and 3). Most species can be distinguished on the basis of their frond morphology, venation pattern and cuticular structure (Tables 2 and 3). Cuticular structures are overall rather similar to one another; however, they can help distinguish species that are less clearly differentiated by their morphology.

On the basis of morphology and cuticle analysis, *Scytophyllum dentatum* Bornemann and *Scytophyllum bergeri* Bornemann have been found to be conspecific (Linnell, 1933; Kustatscher, 2007), and *Scytophyllum rumpfii* (= *Cycadites rumpfii* Compter) is identical to *Scytophyllum apoldense* Linnell (Linnell, 1933). Kustatscher (2007) documented specimens attributed to *Scytophyllum* from northern Italy and concluded that *Scytophyllum bergeri* Bornemann, *S. apoldense* Linnell and *S. dentatum* Bornemann, which differ from each other in their leaf shape, belong to the same natural but variable species, and that *Scytophyllum dubium* Compter, described by Compter (1922), is a later synonym of *S. bergeri* Bornemann. The differences between *S. bergeri* Bornemann and *S. apoldense* Linnell may suggest different exposures to the sun (Kustatscher, 2007).

Scytophyllum karamayense is similar with ten other species all for having interfascicular veins. *Scytophyllum karamayense* can be distinguished from these others based on the characters of the pinna margin, apex, rachis and cuticles (Table 2). The pinna of the new species described herein is similar to that of several other species of *Scytophyllum*, including *S. abramovii* Dobruskina, *S. chaoyangense* Zhang et Zheng, *S. lepidopteroides* Chramova, *S. obovatifolium* Li et He, *S. pinnatum* Dobruskina, *S. shensiensis* Huang et Zhou, *S. tenuinerve* Mogutcheva and *S. wuziwanensis* Huang et Zhou. In *S. karamayense*, the pinna apex is acute and pinna shape is lanceolate with a smooth rachis. Other species generally have an obtuse pinna apex and linear or ribbon shaped pinna. *Scytophyllum lepidopteroides* Chramova and *S. pinnatum* are very similar to *S. karamayense*, but differ in having characteristic rachis features with either hair traces or a lumpy appearance. In *S. abramovii* Dobruskina, most of the pinna characters are unknown but the cuticle is hypostomatic whereas in *S. karamayense* it is amphistomatic.

The cuticle structures of species of *Scytophyllum* are very similar. Most species have amphistomatic leaves, elongate polygonal or isodiametric epidermal cell shape with straight anticlinal walls and thickened periclinal walls, randomly distributed monocyclic stomata with sunken guard cells and 4–7 subsidiary cells (Table 3). Species with distinct cuticular structures include *S. abramovii*, which has hypostomatic leaves; *S. flexuosum*, *S. geniculatum* and *S. sectum* with superficial stomatal apertures; and *S. neuburgianum*, *S. sectum* and *S. waehneri* that lack papillae. The cuticle structures of *S. karamayense* are overall similar to those of most other

species of *Scytophyllum*, but in all cases *S. karamayense* can be distinguished on its straight or curved anticlinal walls with irregular thickening and in bearing a single papilla on each cell except those near the stomatal complex.

In previous studies, stomatal density has been considered as an important character in distinguishing species of *Scytophyllum* (e.g., Bornemann, 1856; Linnell, 1933; Dobruskina, 1969, 1975; Chramova, 1973, 1977). However, stomatal density varies considerably even in a single species; this is noteworthy because stomatal index is typically considered to be a robust taxonomic character (e.g., Dilcher, 1974; Kerp, 1990). However, accurate comparisons of stomatal index among species of *Scytophyllum* are not possible, because stomatal indices have not been reported in recently described species (Morel, 2010; Kustatscher et al., 2011).

4.2 Ecology

Recent investigations of fossil plant assemblages from Kühwiesenkopf (NE-Dolomites, Italy) suggest that *Scytophyllum bergeri* might have been a shrub-like plant with a differentiation in sun and shade leaves, growing in lowland plains in warm and humid climates (Kustatscher et al., 2010). However, the ecology and growth habit of most *Scytophyllum* species from Eurasia are unknown.

During the Middle and Late Triassic, lacustrine deposits were extensively developed in the Junggar Basin suggesting a humid climate in the basin (BGMRX, 1993). Research on the sedimentology and facies analysis of Triassic–Jurassic within the basin provides information on the palaeoclimate: the Triassic to the Early Jurassic

was dominated by humid climates (Ashraf et al., 2010; Bian et al., 2010). Sediments from the Karamay Formation in the Shendigou section in particular consist of alluvial, fluvial and lacustrine deposits indicating that there was abundant water at the time of deposition (e.g., Tang et al. 2015; Luo et al. 2015). According to BGMRX (1993) and Tang et al. (2015), rains and floods occurred seasonally forming alluvial deposits. Red beds intercalated in the studied outcrop indicate that this area may have experienced warm climates with alternating wet and dry seasons (see Walker, 1976; Parrish, 1998; Dubiel and Smoot, 1994). However, Sheldon (2005) considered that continental red beds can also form in warm, humid climates with good drainage. Therefore, such red beds do not necessarily indicate dry conditions. Although the sedimentary analysis indicates that the climate may have been humid with a dry seasonal, the thick cuticle, sunken stomata and the papillae surrounding the stomatal aperture indicate that *Scytophyllum karamayense* may have suffered from water stress, with the cuticle being adapted to reducing water loss (Kerp, 1990).

The records of peltasperms are widespread and abundant in the Permian tropics (Kerp, 1988; Kerp and Haubold, 1988; DiMichele et al., 2005, 2013a,b; Wang et al., 2013; Wan et al., 2016), appearing at least as early as the Late Pennsylvanian. Although the early history of peltasperms is insufficiently understood, all known records indicate that peltasperms probably originated in the tropical extrabasinal areas in Euramerica (Doubinger et al., 1995; Lausberg and Kerp, 2000; Kerp et al., 2001). DiMichele et al. (2013b) inferred that peltasperms occurring in clastic deposits usually grew in seasonally dry environments. However, Kerp and Fichter (1985) and

Barthel and Rößler (1996) demonstrated that some peltasperms, such as *Rhachiphyllum schenkii*, could grow in more humid settings. By contrast, records from Cathaysia indicate that peltasperms could exist in a variety of environments, including those with ever-wet conditions (Wang et al., 2014). *Scytophyllum* may have had a similar growth habit but the present species suggests adaption to water-stressed environments.

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Figure Captions

Figure 1. Location of the Shendi valley section and the sedimentary log of the outcrop. a. Index map showing position of the research area (boxed area) in China. The thick red lines marks the approximate margin of Junggar Basin; b. Locality of research area (boxed area) in the Junggar Basin to the at north of Karamay; c Location of the research area (boxed area); d. Summary geological map showing the formation outcrop patterns and the location of Shendigou section (arrow); e. Sedimentary log of the Upper Karamay Formation, showing the sedimentological context and stratigraphic position of the fossil layer; f. Photo of the outcrop with dashed line marking the position of the fossil plant layer.

Figure 2. Macrocamera setup used for photographing slides to reveal venation pattern.

Figure 3. Venation of leaf taxa with fascicular veins common in the Permian and Triassic. a. *Pachypteris rhomboidalis* Ettingshausen; b. *Fascipteris sinensis* (Stockmans et Mathieu) Gu et Zhi; c. *Fascipteris stena* Gu et Zhi; d. *Validopteris integra* (Gothan) Bertrand; e. *Scytophyllum neuburgianum* Dobruskina. Note that the fascicular veins of *Scytophyllum* are very loose, and their lateral veins do not reach the leaf margin.

Plate I. Holotype of *Scytophyllum karamayense* sp. nov. Scale bars are 10 mm unless otherwise stated. PB 21736.

1. Specimen before maceration showing clear pinna margin but indistinct venation. Arrow indicates area enlarged in Pl. I, 2.
2. Enlargement of pinna margin from arrow in Pl. I, 1 showing dentate margin and indistinct venation. Scale bar = 5 mm.
3. Adaxial cuticle as isolated from the matrix showing the margin and the venation of the lamina. Arrow indicates the interfascicular vein between vein bundles. Slide number PB 21736–1.
4. Adaxial cuticle as isolated from the matrix, with venation marked by lines and indistinct venation was marked by dash lines. Slide number PB 21736-1.
5. Adaxial cuticle from composite photographs merged from 1885 micrographs. Lower part slide number PB 21736–1, the upper part slide number PB21736–2.
6. Abaxial cuticle from composite photographs merged from 1631 micrographs. Lower part slide number PB 21736–3, upper part slide number PB 21736–4.

Plate II. Adaxial cuticle of *Scytophyllum karamayense* sp. nov. showing veins and interfascicular veins. Image enlarged from the top right part of the cuticle shown in Plate I, 4, slide number PB 21736-2. P: midvein; S: secondary vein; T: tertiary vein; Black arrow: interfascicular vein. Scale bar = 400 μm.

Plate III. Adaxial cuticle structure of *Scytophyllum karamayense* sp. nov. enlarged from plate I, 5. Scale bar = 200 μm unless otherwise stated. All images from slide PB 21736–1.

1–2. Detailed structure of costal and intercostal areas, showing cell shape, size and arrangement. Arrows indicate costal areas.

3. Detailed structure of the cuticle on the midrib and the basal part of the secondary vein. The midrib is to the right of the image and the secondary vein is at middle and left of the image. The arrow indicates the cells on the basal part of the secondary vein.

4. Detail of the cells covering interfascicular veins. The black arrows indicate the costal area and white arrow indicates the interfascicular vein area.

5. Detailed structure showing the stomatal apparatus and the ordinary cells in the intercostal area. The black arrow indicates the irregular thickening anticlinal wall. Scale bar = 100 μm.

6. Detailed structure of stomatal apparatus showing subsidiary cells and the papillae surrounding the aperture. Scale bar = 20 μm.

Plate IV. Abaxial cuticle structure of *Scytophyllum karamayense* sp. nov. enlarged from Pl. I, 6. Scale bar = 200 μm unless otherwise stated. Slide number PB 21736–3.

1–2. Structure of the costal (black arrows) and intercostal area, showing cell shape, size and arrangement.

3. Detail showing the structure of the cuticle on the midrib and the adjacent intercostal area. The midrib is shown at the right part.

4. Cuticle showing the marginal structure of the abaxial cuticle.

5 – 6. Showing stomatal apparatus on the abaxial cuticle, and the irregular thickening anticlinal walls. Scale bar = 50 μm.

Plate V. SEM picture of interior and exterior cuticle of *Scytophyllum karamayense* sp. nov. Stub number PB 21736-5.

1. Exterior cuticle showing papillae. Arrow indicates stomatal apparatus. Scale bar = 100 μm.

2. Enlargement from 3 (arrow) showing detailed structure of the papillae raised directly surrounding the stomatal aperture. Sclae bar = 20 μm.

3. Interior cuticle showing structure of stomatal apparatus. Scale bar = 25 μm.

4. Interior cuticle showing the hollow papilla on the ordinary cell and the anticlinal walls. Scale bar = 25 μm.

5-6. Interior cuticle showing the irregular thickening on the anticlinal walls. Scale bar in 5 = 15μm, and in 6 = 25μm.

Table 1. Lithostratigraphy and fossil plant biostratigraphy of the Triassic basin fill successions in the Junggar Basin.

Table 2. Frond characters of species of *Scytophyllum*. *Scytophyllum bergeri* and *S. apoldense* are listed as separate taxa but may belong to the same plant (Kustatscher et al., 2007).

Table 3. Cuticular characters of species of *Scytophyllum*. *Scytophyllum bergeri* and *S. apoldense* are listed as separate taxa but may belong to the same plant (Kustatscher et al., 2007).

Table 1. Lithostratigraphy and fossil plant biostratigraphy of the Triassic basin fill successions in the Junggar Basin.

<table>
<tr><td colspan="5">Stratigraphy</td><td colspan="2" rowspan="2">Plant assemblages</td></tr>
<tr><td colspan="2" rowspan="2">Age</td><td colspan="3">Formation</td></tr>
<tr><td>Yang et al., 1986; Sun et al., 2010</td><td>Lou et al., 2015</td><td>Present study</td><td>Yang et al., 1986</td><td>Sun et al., 2010</td></tr>
<tr><td>Jurassic</td><td>Early</td><td>Badaowan Fm.</td><td></td><td></td><td></td><td>Neocalamites – Marattiopsis assemblage</td></tr>
<tr><td rowspan="5">Triassic</td><td rowspan="3">Late</td><td>Haojiagou Fm.</td><td rowspan="2">Baijiantan Fm.</td><td rowspan="2">Baijiantan Fm.</td><td rowspan="4">Danaeopsis – Bernoullia assemblage</td><td>Glossophyllum – Cycadocarpidium assemblage</td></tr>
<tr><td>Huangshanjie Fm.</td><td>Danaeopsis – Nanzhangophyllum assemblage</td></tr>
<tr><td rowspan="2">Karamay Fm.</td><td rowspan="2">Karamay Fm.</td><td rowspan="2">Karamay Fm.</td><td rowspan="2"></td></tr>
<tr><td>Middle</td></tr>
<tr><td rowspan="2">Early</td><td>Shaofanggou Fm.</td><td rowspan="2">Baikouquan Fm.</td><td>Shaofanggou Fm.</td><td></td><td></td></tr>
<tr><td>Jiucaiyuan Fm.</td><td>Jiucaiyuan Fm.</td><td>Pecopteris sp.</td><td></td></tr>
</table>

Table 2. Frond characters of species of *Scytophyllum*, *Scytophyllum bergeri* and *S. apoldense* are listed as separate taxa but may belong to the same plant (Kustatscher et al., 2007)

Species	Locality	Age	Rachis	Pinna						Reference
				Shape	Margin	Apex	Base	Lateral vein	Suture vein	
S. karamayense	Karamay, China	Middle-Late Triassic	smooth	lanceolate	dentate	acute	constrict	fascicular	simple	Present paper
S. abramovii Dobruskina	Pechora, Russian	Late Triassic	smooth	—	entire - undulate	—	—	fascicular	simple	Dobruskina, 1969
S. apoldense Linnell	Germany, Russia	Late Triassic	smooth	lanceolate	entire	obtuse	decurrent	fascicular tertiary vein branch	absent	Linnell, 1933; Dobruskina, 1969
S. argentinum Morel	Mendoza, Argentina	Late Triassic	lumpy	linear – lanceolate	lobate	acute	decurrent coherent	fascicular	absent	Morel, 2010
S. austroafricamum Anderson et Anderson	South Africa	Triassic	—	linear	partite	—	—	fascicular quaternary veins	fascicular complex	Anderson & Anderson, 2003
S. baschkiricum Dobruskina	Southern Urals	Late Triassic	lumpy, winged	linear	undulate	obtuse	decurrent	fascicular	absent	Dobruskina, 1969
S. bergeri Bomemann	Thuringia, Germany	Late Triassic	smooth winged	linear	partite	obtuse	decurrent coherent	fascicular	absent	Bornemann, 1856
S. bonettiae Zamuner et al.	Argentina	Middle Triassic	lumpy winged	lanceolate	lobulate - dentate	acute	decurrent coherent	fascicular	absent	Zamuner et al., 1999
S. chaoyangense Zhang et Zheng	Liaoning, China	Late Triassic	smooth	oblong - lanceolate	entire - undulate	obtuse	decurrent	fascicular	simple or bifurcate	Zhang and Zheng, 1984
S. flexuosum Chramova	Pechora, Russia	Late Triassic	smooth	lanceolate	entire - undulate	obtuse	constrict or petiole	fascicular	absent	Chramova, 1973; Kiritchkova & Ensenia, 2014
S. geniculatum Chramova	Pechora, Russia	Late Triassic	smooth, winged	lanceolate	undulate	—	constrict	fascicular	absent	Chramova, 1977
S. karevae Kiritchkova et Chramova	East Ural, Russia	Late Triassic	smooth, winged	lanceolate	dentate	obtuse	decurrent	fascicular, branched	absent	Kiritchkova & Chramova, 1981
S. kolvaense Chramova	Pechora, Russia	Middle – Late Triassic		oblong	lobulate	obtuse	—	fascicular	absent	Chramova, 1973
S. kuqaense Wu et Zhou	Tarim Basin, China	Early Triassic	smooth	oblong - linear	entire	—	decurrent	fascicular	absent	Wu and Zhou, 1990
S. lepidopteroides Chramova	Pechora, Russia	Late Triassic	with hair trace	oblong - lanceolate	entire - undulate	—	decurrent	fascicular	Simple or bifurcate	Chramova, 1977; Kiritchkova & Ensenina, 2014
S. multipapillatum Chramova	Pechora, Russia	Late Triassic	—	—	—	—	—	—	—	Chramova, 1977
S. nerviconfluens Dobruskina	Western Kazakhstan	Late Triassic	smooth	ribbon	entire - undulate	acute	decurrent	fascicular	absent	Dobruskina, 1969
S. neuburgianum Dobruskina	Pechora, Russia	Late Triassic	—	linear	undulate	obtuse	—	fascicular	simiple	Dobruskina, 1969
S. obovatum Huang and Zhou	Shaanxi, China	Triassic	with longitudinal striate, winged	ovate	entire - undulate	obtuse	decurrent	fascicular	absent	Huang & Zhou, 1980
S. obovatifolium Li et He	Qinghai, China	Late Triassic	smooth	oblong - lanceolate	dentate	obtuse	constrict	fascicular	simple or bifurcate	Li & He, 1986
S. papillosum Dobruskina	Pechora, Russia	Late Triassic	smooth	linear - ligulate	undulate	obtuse	—	fascicular, tertiary veins dense	absent	Dobruskina, 1969
S. sectum Chramova	Pechora, Russia	Late Triassic	smooth	lanceolate - ligulate	entire	acute	constrict	fascicular	absent	Chramova, 1977
S. shensiense Huang and Zhou	Shaanxi, China	Triassic	With longitudinal striate and middle rib, winged	ribbon	entire	obtuse	decurrent	fascicular	simple	Huang & Zhou, 1980
S. tenuinerve Mogutcheva	Tunguska, Russia	Early Triassic	with longitudinal	linear	dentate	obtuse	decurrent	fascicular	simple	Mogutcheva, 1973

S. vulgare Kiritchkova et Chramova	East Urals, Russia	Late Triassic	striate, winged smooth	linear	entire	obtuse	—	fascicular	absent	Kiritchkova & Chramova, 1981
S. waehneri (Stur) Kustatcher	—	Late Triassic	smooth	lanceolate	entire - undulate	acute - obtuse	constrict	fascicular	absent	Kustatscher, 2011
S. wuziwanense Huang and Zhou	Inner Mongolia	Triassic	lumpy	oblong - linear	undulate - dentate	obtuse - acute	decurrent	fascicular	simple	Huang & Zhou, 1980

Table 3. Cuticular characters of species of *Scytophyllum*. *Scytophyllum bergeri* and *S. apoldense* are listed as separate taxa but may belong to the same plant (Kustatscher et al., 2007).

Species	Leaf type	Cuticle (upper/lower)							Reference
		Stomata				Cell shape	Anticlinal wall	Ornamentation	
		Type	Distribution	Density (upper/lower per 1 mm^2) or index	Subsidiary cells				
S. karamayense sp. nov.	amphistomatic	sunken, monocyclic	random	index 3.27/5.25 density 15/30	4-6, usually 5, papillate	enlongated polygonal	straight or curved, with irregular thickening	one papilla present on each cell, but except those near stomatal complex	Present paper
Scytophyllum abramovii	hypostomatic	sunken, monocyclic	in costal area	0/30	4-6, papillate	elongate polygonal	straight	one papilla present on each cell	Dobruskina, 1969
S. apoldense	amphistomatic	sunken, monocyclic	random	5-10/13-16	4-7, papillate	elongate polygonal	straight	papilla absent on ordinary cells	Linnell, 1933; Dobruskina, 1969
S. argentinum	amphistomatic	sunken, monocyclic	random	—	4-7, papillate	polygonal and rectangular	straight	one papilla present on each cell	Morel, 2010
S. austroafricamum	—	—	—	—	—	—	—	—	Anderson and Anderson, 2003
S. baschkiricum	amphistomatic	sunken, monocyclic	random	45/70	4-5,papillate	polygonal	straight or undulate	one papilla present on each cell	Dobruskina, 1969
S. bergeri	amphistomatic	sunken, monocyclic	random	(fewer than lower cuticle)/100-200	6, without papillae	pentagonal and hexagonal	straight	absent	Bornemann, 1856
S. bonettiae	—	—	—	—	—	—	—	—	Zamuner et al., 1999
S. chaoyangense	—	—	—	—	—	—	—	—	Zhang and Zheng, 1984
S. flexuosum	amphistomatic	unsunken, monocyclic	random	0/40-50	5-6, papillate	elongate polygonal and isodiametrical	straight, irregularly cutinized	one papilla or warty on each cell	Chramova, 1973; Kiritchkova and Ensenia, 2014
S. geniculatum	amphistomatic	unsunken, monocyclic	upper side random; lower side longitudinal oriented	0/40-50	upper side 5-6; lower side 5-7, papillate	polygonal – enlongated polygonal	straight or undulate	papillae absent on upper side,	Chramova, 1977; Kiritchkova and Ensenia, 2014
S. karevae	amphistomatic	sunken, monocyclic	random	—	5-6, papillate	polygonal and isodiametric	thin, straight or undulate	one papilla or hollow papilla on each cell	Kiritchkova and Chramova, 1981
S. kolvaense	amphistomatic	sunken, monocyclic	random	25/35-40	5-6, without papillae	elongated polygonal and	straight or undulat	one papilla on each cell	Chramova, 1973

						isodiametric	e		
S. kuqaense	—	—	—	—	—	—	—	—	Wu and Zhou, 1990
S. lepidopteroides	amphistomatic	sunken, monocyclic	upper side in costal area; lower side in intercostal area	—	4-7, usually 5-6, papillate	quadrangular and isodiametric	straight	papillae or warty	Chramova, 1977; Kiritchkova and Ensenina, 2014
S. multipapillatum	amphistomatic	sunken, monocyclic	random	20-25/50-60	4-7, papillate	polygonal	straight	several papillae on each cell	Chramova, 1977
S. nerviconfluens	amphistomatic	sunken, monocyclic	random	30/30	4-7, usually 5, papillate	elongated polygonal	straight or undulate	one papilla on each cell	Dobruskina, 1969
S. neuburgianum	amphistomatic	sunken, monocyclic	random	12/30	5-6, papillate	polygonal	straight or undulate	papillae absent	Dobruskina, 1969
S. obovatum	—	—	—	—	—	—	—	—	Huang and Zhou, 1980
S. obovatifolium	—	—	—	—	—	—	—	—	Li and He, 1986
S. papillosum	amphistomatic	sunken, monocyclic	random	10-20/25-30	5-6, papillate	polygonal	straight or undulate	two or three papillae on one cell	Dobruskina, 1969
S. sectum	amphistomatic	unsunken, monocyclic	random	20/30	4-7, papillae absent	polygonal, elongated polygonal	straight or undulate	papillae absent	Chramova, 1977
S. shensiense	—	—	—	—	—	—	—	—	Huang and Zhou, 1980
S. tenuinerve	—	—	—	—	—	—	—	—	Mogutcheva, 1973
S. vulgaris	amphistomatic	sunken, monocyclic	random	—	4-6, usually 5-6, papillate	round, isodiametric, elongated polygonal	straight, irregular thickening	papillae present	Kiritchkova and Chramova, 1981
S. waehneri	amphistomatic	sunken, monocyclic	along the costal area	—	usually 6, papillate	elongated polygonal, isodiametric, trapezoid	straight, thick	papillae absent	Kustatcher, 2011
S. wuziwanensis	—	—	—	—	—	—	—	—	Huang and Zhou, 1980

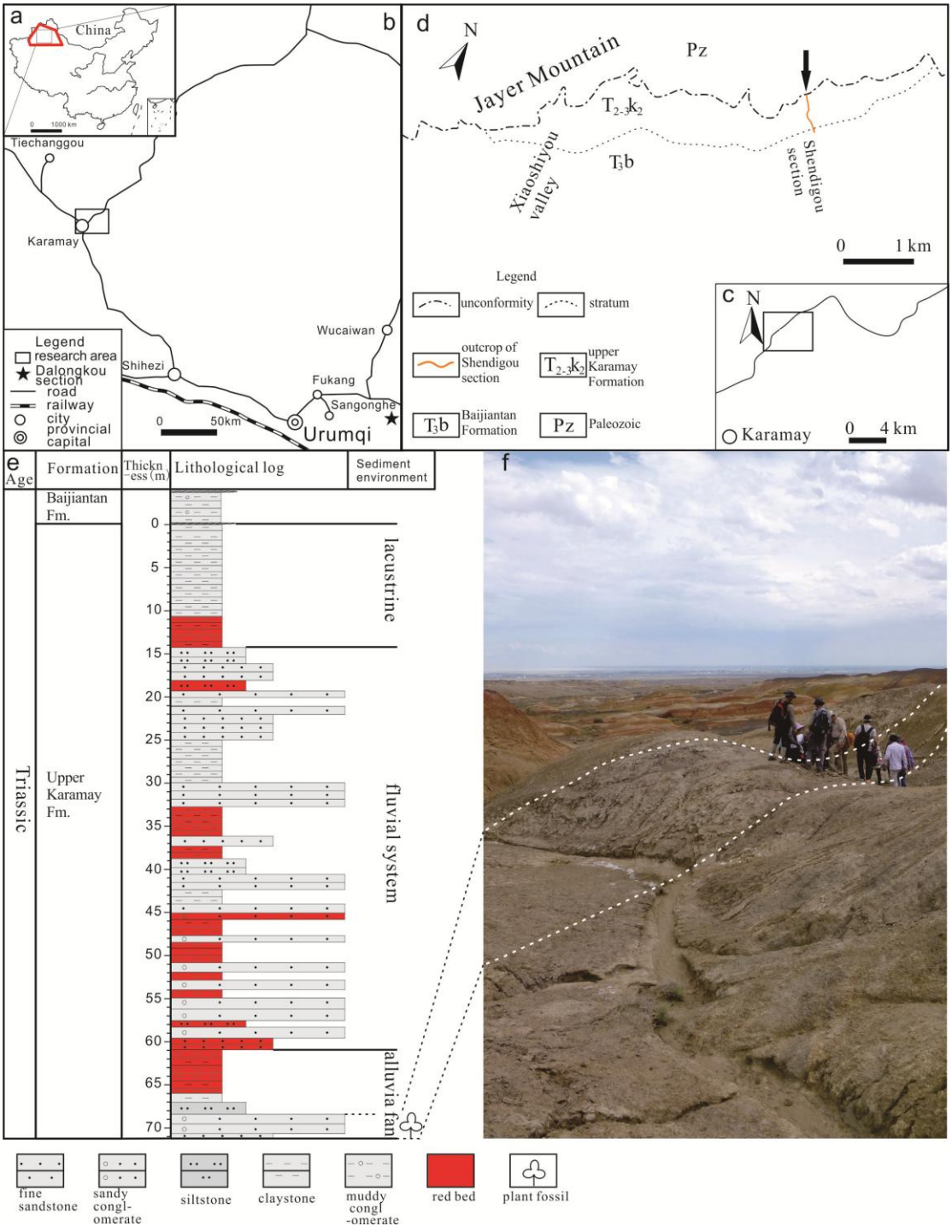

Figure 1

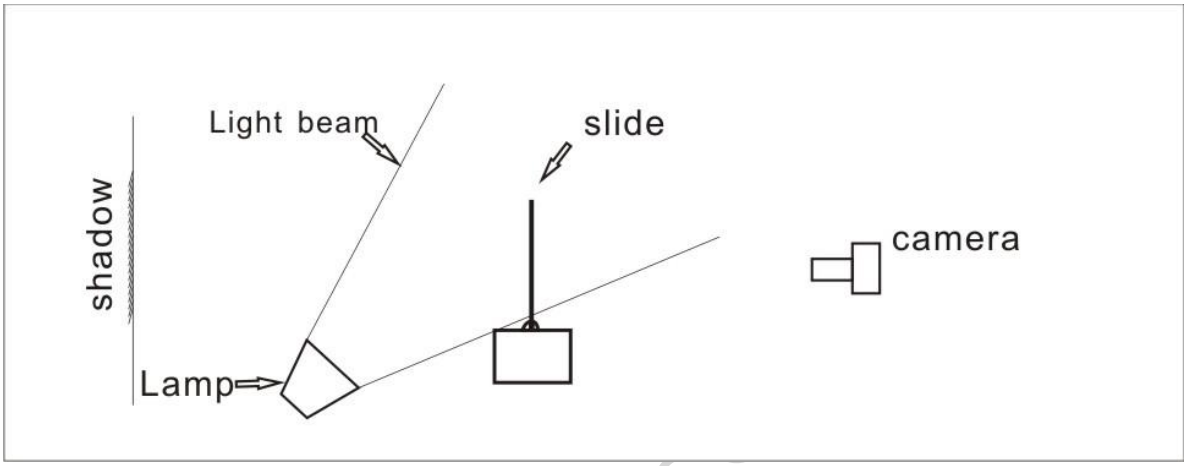

Figure 2

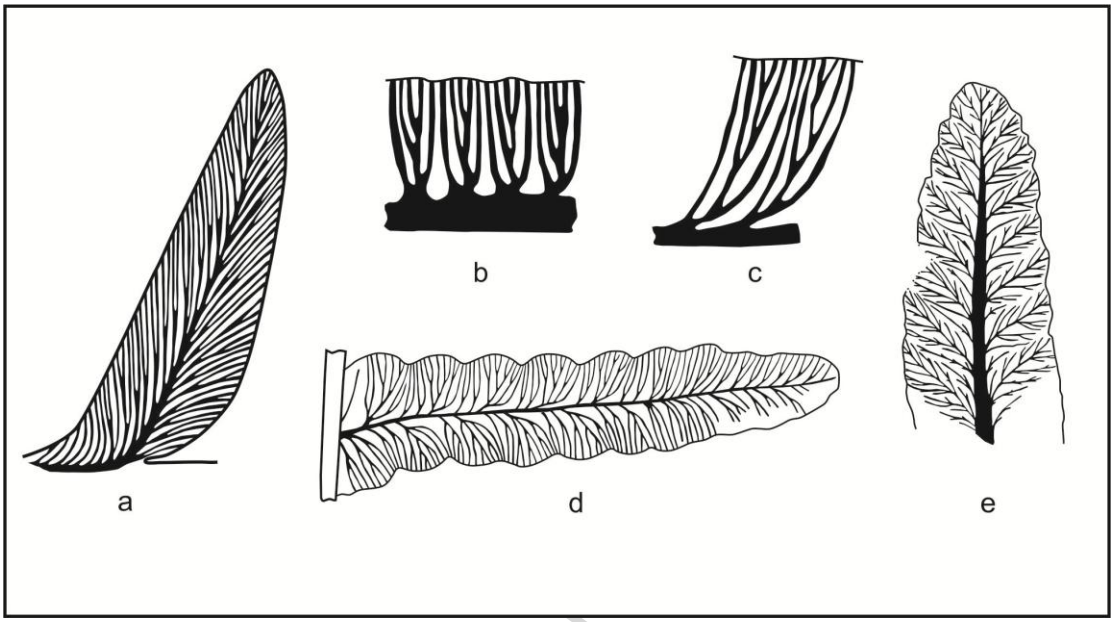

Figure 3

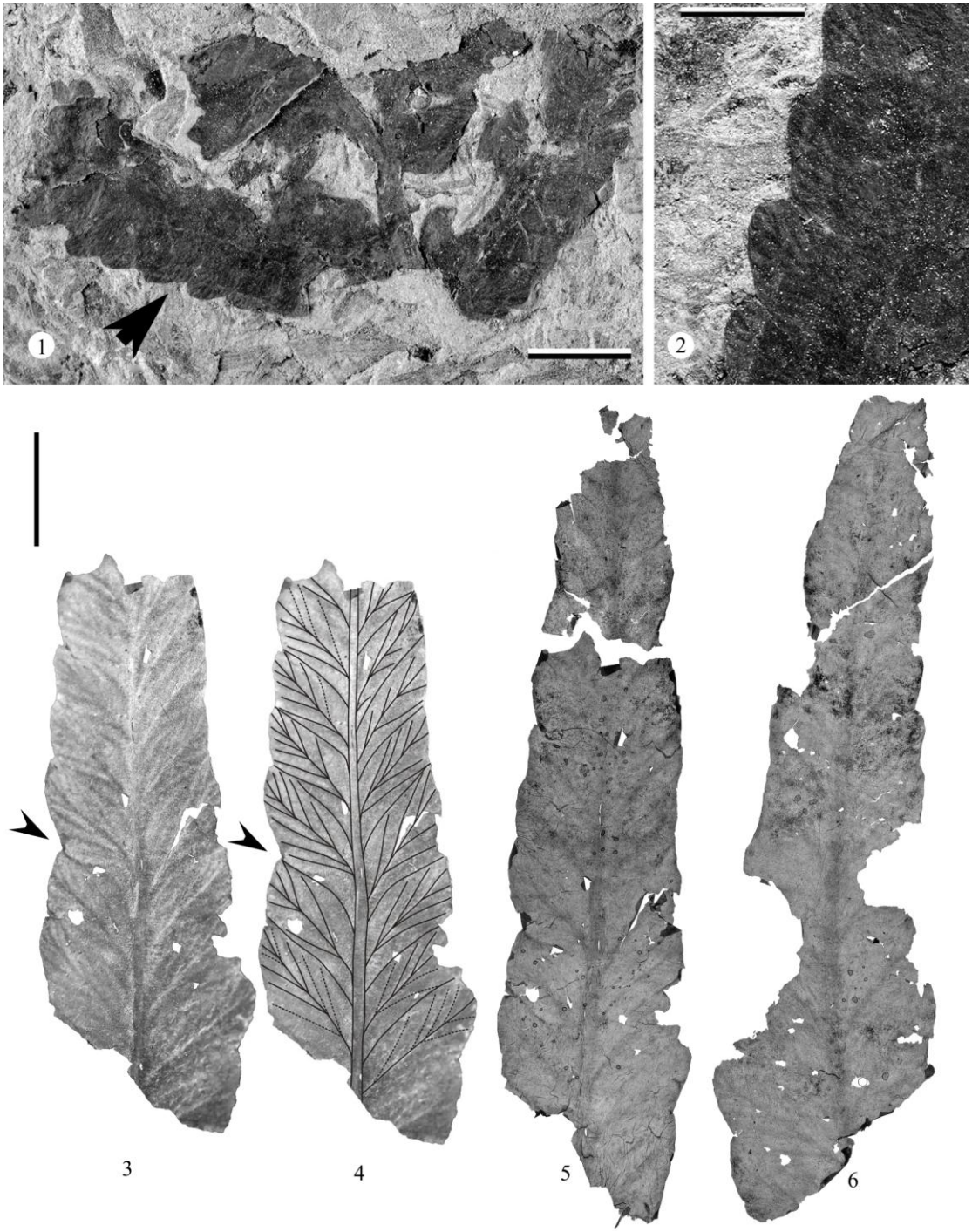

Plate I

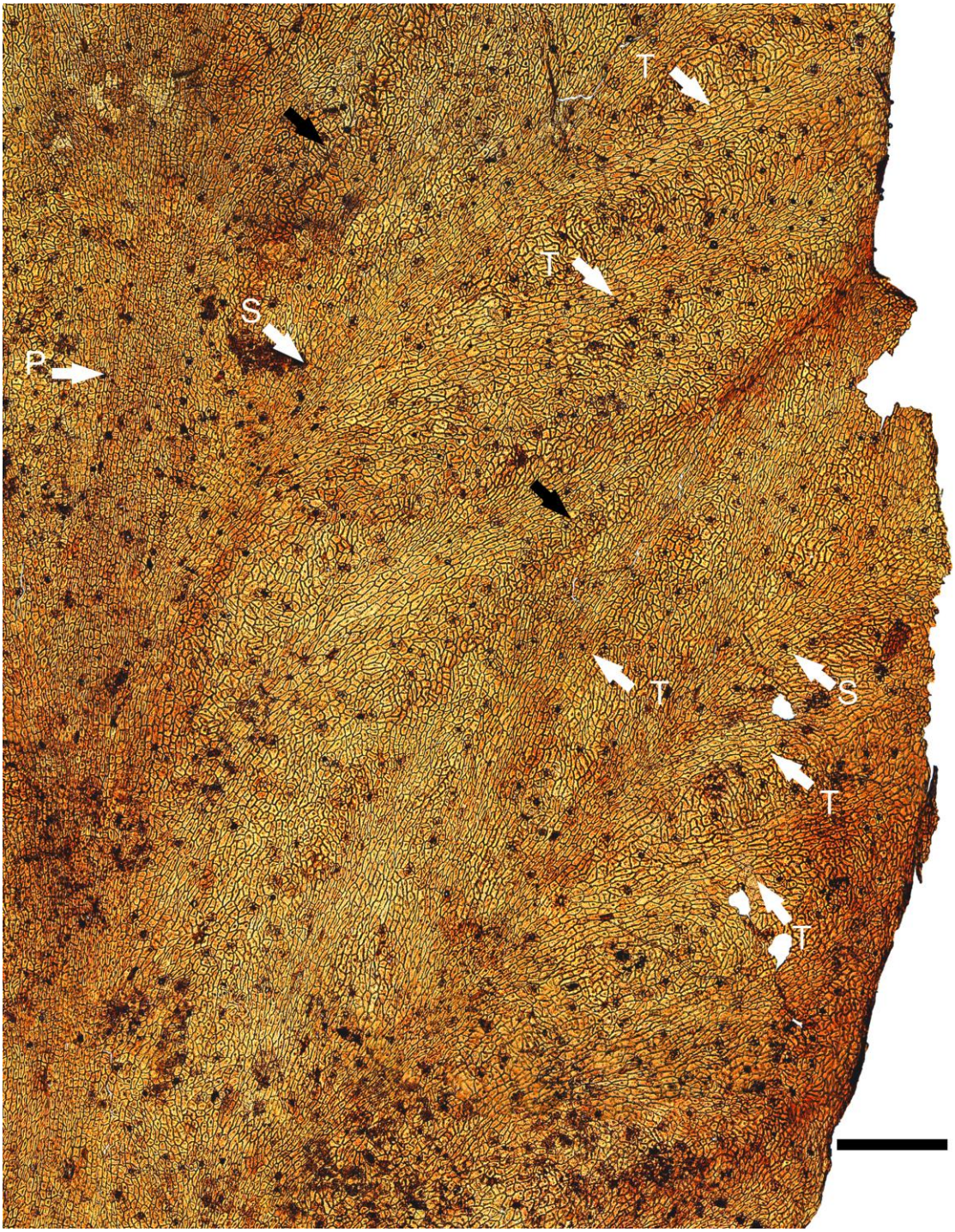

Plate II

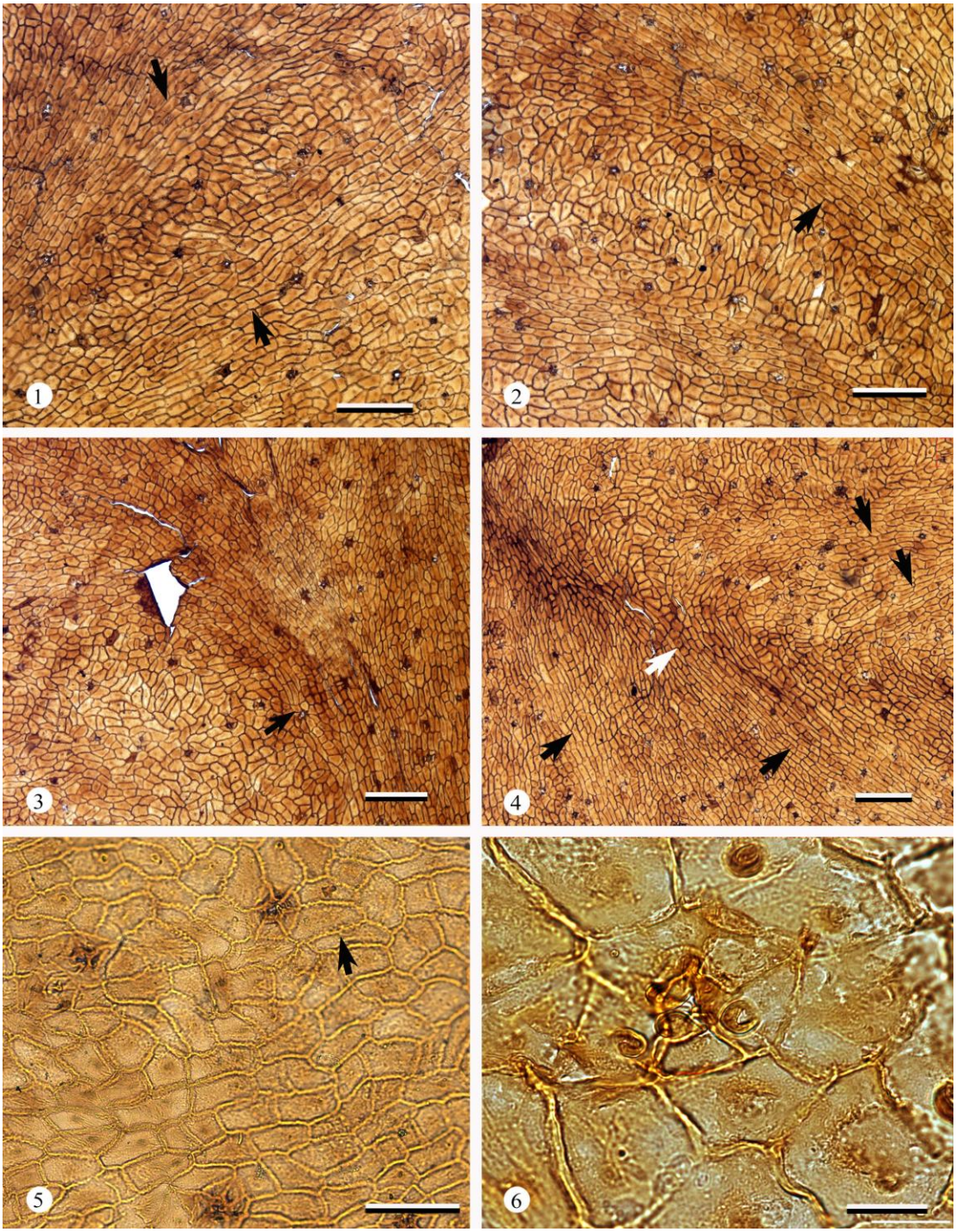

Plate III

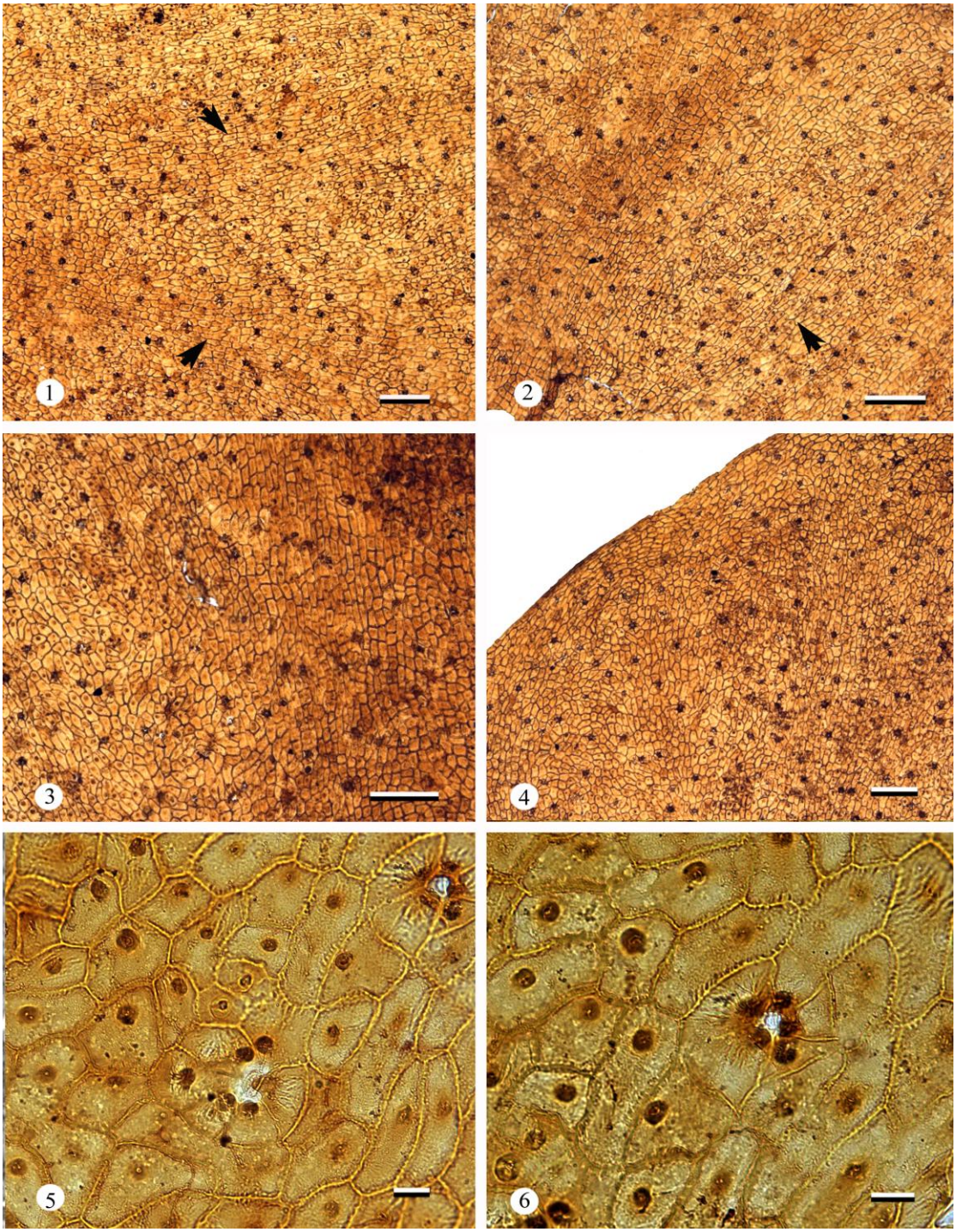

Plate IV

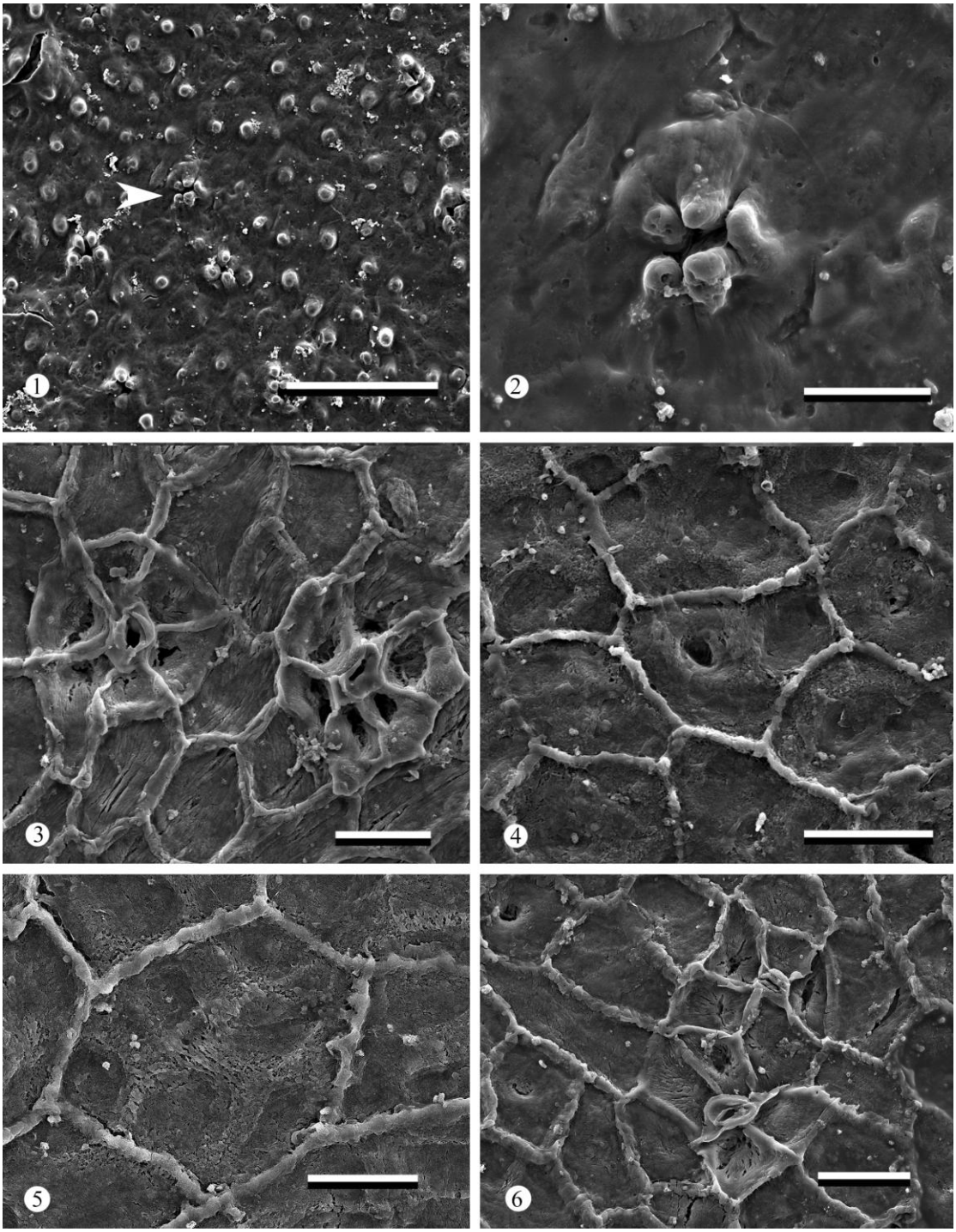

Plate V